THE LARVAE OF OESTRIDAE.

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The larvae of the *oestridae*, although in many cases quite peculiarly shaped, are so nearly related to the larvae of the rest of the *muscidae-calyptera* that it has not yet been possible to discover for them a constant distinguishing character founded upon their structure. The reason of this lies in part in the oestrid larvae themselves, since they are very different among themselves, and in part also in our defective knowledge of the muscid larvae.

At present, it is true, no real muscid larvae are known with large thornwarts,—as I will call the dermal formations which occur in many oestrid larvae, which are conical, soft at the base, fleshy, and corneous at the tip,—also none with the characteristic stigmatal plate of the *Gastrophilus* larvae; on the other hand very many are known with thorns, like those of *Dermatobia*, or naked, like those of the young *Hypoderma*, or with horny stigmatal plates, like those of *Cephenomyia*. The remarkable parasitic method of life in mammals can probably be looked upon as peculiar to the *oestridae*. I leave it therefore to a future observer to establish a character for the oestrid larvae whereby they may be distinguished from all other muscid larvae, and limit myself here to the description of the larvae according to genera and species.

The oestrid larvae belong to the great division of those dipterous maggots which have been called headless, since they are segmented throughout and the usual regions of the insect body are not separated. Only a cephalic and an anal end, therefore, can be distinguished on the annulate body of such larvae. In general the following common characters and peculiarities of the oestrid larvae can be specified.

1. The body of all oestrid larvae is really composed of twelve rings. The first two are however not always distinctly separated, so that I take them together in the description, and designate them both by the name of cephalic ring, on which in many cases an anterior and posterior section is clearly to be distinguished. On that account I assume only eleven segments, as earlier authors have done. Only the newborn larvae of *Gastrophilus* make an exception to this number; they, if Joly's statement is correct, possessing thirteen segments.

2. Two anterior, external breathing-organs are always to be distinguished on the larvae, between the first and second segments of the body, and two posterior, external breathing-organs on

the last ring. The former are very small and appear either as points, knobs or fissures, or the anterior ends of the tracheae are hidden entirely in a cylindrical invagination of the skin (*Gastrophilus*). The posterior breathing-organs are either breathing-tubes which are protrusile and retractile (new-born *Gastrophilus* [p. 36] larvae and *Cephenomyia* larvae), or large stigmatal plates which are constructed according to two kinds of types. One of these types is represented in *Gastrophilus* and *Dermatobia*, the other in the rest of the genera. The stigmatal plates are more or less protected by lip-like organs on the last ring or by withdrawal into the preceding ring, and are in this way cleaned from substances which adhere to them.

I have described in detail under that genus the structure of the posterior stigmatal plates in *Gastrophilus*. The majority of the genera possess however two stigmatal plates in a real sense, consisting of corneous chitinous substance on the last ring. Each ring is usually crescent-shaped or reniform, in younger larvae even quite circular, and appears when magnified either as latticed with coarse meshes, finely porous or almost smooth, sometimes radially furrowed. On the inner border of each plate is in all larvae in the third and in many in the second stage a thinner, membranous or knob-like place superposed or imbedded, sometimes enclosed in the plate itself. The attachment of the trachea corresponds to this place on the inside. Since it usually has the appearance of an opening, and also has been taken for such, I call it the false stigmatal opening. It has not yet been ascertained without doubt that breathing goes on in such stigmatal plates, but it probably takes place through pores of the plate. It seems to me as if the plates were penetrable especially at the circumference of the attachment of the tracheae.

3. The new-born larvae all possess external mouth-parts; in the later stages larvae with oral hooks and those without them are to be distinguished. An internal pharyngeal framework of various development always occurs; this encloses the membranous gullet and by its muscular structure is of essential service in the sucking of the larva. If oral hooks are present, they are connected with this by a joint.

Usually a U-shaped, bent chitinous plate is to be seen, whose open side looks upward; from the side it has the shape of a sitting butterfly whose large upper wing reaches far back and has the smaller, narrow under wing under it. Since the wings of the two sides are grown together firmly underneath, the whole pharyngeal framework appears like a flying insect, when the wings are bent apart from above, and with the base in a plane. The part lying more or less in front, which is to be found in the middle between the wings, and which really radiates out into these, or is united with them like a ligament, is what Schroeder van der Kolk calls the tongue-bone.

In the pharyngeal framework there-

fore there can be recognized a body (Schroeder's tongue-bone) and four wing-like processes which often again consist of several parts. The body is connected with the wings posteriorly. It is always bent in a U-shape, and so that the open end looks upward, *i.e.*, if other soft parts of its vicinity which also close this are disregarded. [p. 37] Bent flat, it shows a more or less distinctly H-shaped chitinous plate, with very broad side parts, which—in full-grown larvae—become confluent behind into a simple, broad plate, and only leave an oval hole in front of them for the passage of the discharge duct of the salivary glands, but posteriorly bear the four wing-shaped processes (two large upper, or in the outspread plate outer ones, and two smaller, slenderer inferior or inner). On the anterior end of the body, in many genera, oral hooks are jointed to the short anterior side parts. In the anterior curved excavation of this lies in the membranous expansion a small corneous chitinous plate which is pierced like a sieve and whose nature has not yet been more closely investigated. It seems to me as if this plate lay at the outlet of the salivary ducts. It is especially distinct in *Cephenomyia* larvae. It is wanting in several others.

In young larvae the pharyngeal framework consists only of two chitinous rods which are united in front by a chitinous band; these chitinous rods radiate out behind in little wings. A (similar) pharyngeal framework occurs in all other muscid larvae, and corresponds in the perfect insect to the chitinous frame of the proboscis. I have repeatedly convinced myself that such is really the case, since I have opened the coarctate pupae of *Cephenomyia* and *Gastrophilus* before the emergence of the flies. Since in these genera, as we will see later, the nymph is tightly enclosed by the puparium, it can be noticed how the already freed pharyngeal framework, which remains attached to the puparium, rests in the mouth-fissure of the nymph, and is drawn out of it as soon as the nymph is taken away or the lower lid is lifted off. It is also easy to form an idea that the pharyngeal framework together with its internal parts corresponds to the proboscis of the fly if it is observed how other muscid or syrphid larvae while alive project and withdraw this exactly as the fly does its proboscis.

In *Hypoderma* the mouth-parts undergo a retrograde metamorphosis from the second stage (after the first molt); the oral hooks disappear, and therewith all the external mouth-parts, but the internal pharyngeal framework remains.

4. The oestrid larvae show antennae (at least rudimentary ones) above the mouth-parts; these have the appearance of corneous or usually membranous knobs, and in the latter case are provided with one or two ocelli-like points. Subulate, many-jointed antennae, such as occur in many muscid larvae, are never found.

5. All possess an anus, which lies on the last ring, under the stigmatal plates, and is very small.

6. They molt twice while they are parasitic. I have observed most closely the molting in *Hypoderma* larvae of the second stage. In *H. diana* the passage from this stage [p. 38] to the last one takes place about the beginning of February. If in a cutaneous muscle which is richly larded with such larvae the capsules of those larvae whose hinder stigmatal plates have the shape of the third stage, but are still clear yellowish-brown, are carefully slit open, the skin characteristic of the preceding stage, with the many little thorns heaped in groups, will be found either still partly attached to the front end of the larva or entirely dependent from the cephalic end or folded together along the dorsal side. The process of molting seems to be entirely similar to that in the *Melophagus* larvae; at least Leuckart states that the old skin in these is shoved together toward the cephalic end of the larvae and there remains attached. The *Hypoderma* larva, immediately after the molt, is pure white, very soft, and appears naked, since the thorns do not become dark and distinctly separated from their surroundings until they harden.

Three forms or stages are to be distinguished, corresponding to the molts, which forms in *Hypoderma*, *Gastrophilus* and *Dermatobia* show great differences. In the third stage the larvae reach their full size, usually change their color and that often very considerably, and then first leave their host-animal, crawl away and pupate, after the manner of the *muscidae*.

7. This pupation must be considered as a third molting, in which, however, the skin is only detached around the pupa, but is not stripped off, and remains in connection with it by means of four tracheae. The hardened larval skin, or puparium, is burst open at the cephalic end by the emerging fly by means of the frontal bladder filled with fluid, in the direction of the arcuate sutures in a double manner. Although the pupation resembles herein that of the *muscidae* in general, yet there occurs in one part of the *oestridae*, *i.e.*, in *Hypoderma*, a peculiarity which has not been observed before, namely, that the larva transforms in the puparium in a completely outstretched condition, and this therefore is far larger than the insect which comes forth from it.

8. So far as they have been observed, they lead a parasitic life in mammals, and feed upon the juices of these animals. In *Hypoderma* a blood-red intestine often shows through, and it is likely that these sometimes suck up blood in addition to the exudation which immediately surrounds them.

9. The closely observed larvae all show at first a slow and finally a rapid development, so that there occurs a resting stage which often lasts seven months, between the swarming of the imago and the first visible appearance of the larvae.

The larvae of the *oestridae* were formerly divided into two groups: into larvae with oral hooks and those without external mouth-parts. Such a separation is of service in distinguishing the

full-grown larvae, but scientifically unnatural and incorrect, since in the first place this peculiarity of the full-grown larvae corresponds to no similar degree of relationship of the perfect insects, and in the second place it is only temporary, [p. 39] since all oestrid larvae possess oral hooks when they are quite young. Such a division also as Clark attempted to make, into *cavicolae*, *cuticolae*, and *gastricolae*, is inadequate, for while the species of a genus do indeed always agree in life-history so far as their occurrence as parasites in a determinate organ is concerned, nevertheless the larvae of very different genera may also share this same manner of life with others; for instance, *Hypoderma*, *Cuterebra*, *Dermatobia*, among which there is far more difference between 1 and 2 than between *Cuterebra* and *Cephenomyia*, if the imagines are considered. Such a division is therefore likewise not a natural one, since it disturbs the natural relations of affinity. Two elements must be considered, in order to bring about an approximately natural division: in the first place the organization of the larvae, and in the second place their manner of life; and the latter in a subordinate degree, though this is here more important than in other animals, since as yet there is no example of two species of *oestridae* of one genus having been found parasitic in different systems of organs. Thus the *Cephenomyia* larvae belong to the oesophagus, the *Cephalomyia* and *Oestrus* larvae to the nasal and frontal cavity, those of *Gastrophilus* to the intestinal tract, and those of *Hypoderma* to the subcuticular cellular tissue.

Although it is stated that the larva of *Gastrophilus* has been found in the oesophagus, this is one of the exceptional cases which are not authenticated. Of course only the full-grown larva is meant here, since young larvae may always be found in other places during the immigrations. So for instance the young *Oestrus* and *Cephenomyia* larvae both immigrate in like manner through the nose, and their roads do not separate until they get there, but the former migrate into the frontal cavity, and the latter into the oesophageal cavity.

Of the organs in which *oestridae* occur, the skin, or really the subcuticular cellular tissue, is that which is the most strongly attacked; the larvae of four genera: *Hypoderma*, *Oestromyia*, *Dermatobia*, *Cuterebra*, live in it. The nasal and frontal cavity are inhabited by the genera *Cephalomyia* and *Oestrus*, the nasal and oesophageal cavity by the genus *Cephenomyia*, the intestinal canal by the genus *Gastrophilus*. The transformations of the other genera of *oestridae* are unknown.

It is interesting farther that many genera occur only as parasites of certain families of mammals, while others have a somewhat wider or very wide range of distribution, and so have for hosts the different mammals, yet not quite without choice, and often even seek men for their breeding places.

Thus until now the larvae of *Cephe-*

nomyia have only been found in the throats of *cervina*, those of the genera *Cephalomyia* and *Oestrus* only in *tylopoda* and *cavicornia*, those of the genus *Gastrophilus* in *solidungula* and *multungula* (*Rhinoceros*), but *Hypoderma*, on the other hand, in *cavicornia* (*Bos*, *Capra*, *Antilope*), *cervina* (*Cervus*, *Moschus*), and *equida*, *Cuterebra* larvae in *rodentia* and *marsupiala*, and finally those of *Dermatobia* in dogs, oxen, horses, and even upon man.

[p. 40] Another picture is formed if the perfect insects are divided according to a peculiar character into those with pectinate antennal bristles (*Cuterebra*, *Dermatobia*), and those with naked antennal bristles (*Hypoderma*, *Gastrophilus*, *Cephenomyia*, *Cephalomyia*), since the larvae of the former are parasitic in ungulate animals as well as especially in *rodentia* and *marsupialia*, but those of the latter only in *ungulata*. This hitherto so convenient and practical division likewise cannot be relied upon for an inference, since *Oestrus leporinus* belongs to the group of *oestridae* with naked bristle, but its larva lives upon a rodent. It is seen that such divisions are only artificial and serve for orientation, but that nevertheless nature cannot be forced into them. Such divisions are therefore only temporary, and only too often become untrue so soon as new discoveries are published. It is therefore best to treat of the larvae according to their genera, and to limit these as naturally as possible, since it has thus far been found constantly in this family that the larvae of one genus all have a like life-history, and conversely the generic characters of the imagines can scarcely lead us astray if we wish to draw an inference as to the life-history of a larva perhaps not yet investigated. In the case of a new genus, however, we can infer its life-history with very little certainty. Experience alone teaches this.

Waxy secretions of psyllid larvae. Dr. Franz Löw, in his "Beiträge zur kenntniss der jugendstadien der psylliden" (Verhandl. K.-k.zool.-bot. gesells., 1884, v. 34; Abh.), p. 144, thus describes a curious secretion in the larvae of *Psylla ulmi*: "From wax-glands surrounding the anus the larva emits a white secretion, which appears as a hollow, vermiform thread that allows the passage through it of the fluid excrement of the larva. This white thread, which reveals the presence of the larvae hidden in the axils of the leaves behind the stipules, elongates continously, but breaks off repeatedly on account of its own weight and consequently reaches no very considerable length. Furthermore this larva secretes from the wax-glands on the dorsal surface of the last abdominal segment extremely fine white threads, which form unitedly a very loose, light flock." The larvae of *Trioza*, three species of which larvae are described in the same paper, have their entire outer margin surrounded by hyaline, silky, very fine, threads of wax, which lie close to one another, and seem to form a short, closely-trimmed fringe around them.